THE CONDUCTING SYSTEM OF THE BIRD'S HEART

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INTRODUCTION

The existence of a specialised form of muscle tissue connecting the auricles and ventricles of the bird's heart, and analogous with the bundle of His and Kent of the mammalian heart, has been denied by many investigators. Furthermore, there is considerable divergence of opinion regarding its disposition among those who have satisfied themselves of the existence of a special avian conducting system.

Tawara (1), Obermeier (2) and Hofmann (3) found numerous large Purkinje fibres in the ventricles, not only in the sub-endocardial connective tissue but also running into the depths of the myocardium with the larger arteries. Keith, Mackenzie and Robertson (4 and 5) after an extensive investigation of the hearts of Vertebrates came to the conclusion that the auriculo-ventricular bundle, as a specialised strand, is peculiar to Mammals. These authors also deny the existence of sinu-auricular and auriculo-ventricular nodes as specialised structures in the bird's heart, though they noted an intimate association between nerve and muscle in the regions of junction of sinus and auricle and of auricle and ventricle. Kulb (6) found a tract of tissue in the bird's heart, resembling in structure the mammalian A.-V. bundle, running across the A.-V. junction at its posterior part and thence prolonged forwards and downwards to join the musculature of the ventricular septum after a short course. Mackenzie (7) found a bundle of "muscle and nerve tissue" passing from the right auricle to the right ventricle only, and Flack (8) showed that when this bundle was ligatured complete A.-V. dissociation occurred. Florence Buchanan's observations on the electro-cardiograms of the bird also suggested that the route of contraction differs in the bird, where the bundle (according to Mackenzie) descends on the right side only, from that in the mammal where the bundle descends on both sides. Mackenzie also found occasional strands of muscular connection between the right auricle and the right ventricle over the free edge of the muscular valve. No such direct muscular continuity was observed on the left side where the parietal valve is membranous and continuity intercepted by a fibrous ring. Mangold and Kato (9) performed a series of cutting and ligaturing experiments at the A.-V. junction of the heart of the fowl and noted the effects produced upon the subsequent electro-cardiograms. They concluded that the following structures are present in the bird's heart: sinu-auricular node near the termination of the right superior vena cava, and auriculo-ventricular bundle with two terminal branches in the ventricular septum. However, they could find no histological differentiation of any specialised muscle tissue in the above sites. Lewis (10) deduced from his electrical studies of the spread of the excitatory process in the bird's heart that the spread, from its rapidity, must be through a special distributing system as in Mammals, and that the supply of specialised tissue to the right and left ventricles is separate as in the mammalian heart. Tang (11), from his study of the minute structure of the Purkinje fibres in the bird's heart, concluded that they are specially modified parts of the conducting system (Reizleitungssystem) and not, as Retzer (12) asserted in the case of the mammalian Purkinje system, embryonal growth centres for the replacement of cardiac musculature. Clark (13), in discussing the conduction in the bird's heart, states that the Purkinje fibres do not form a definite connecting strand between auricle and ventricle, and that the significance of the large Purkinje fibres in auricles and ventricles for the conduction of excitation is therefore obscure. Drennan (14) made naked-eye dissections of the A.-V. bundle in the ostrich heart. No A.-V. node was seen, though a rich nerve supply from the right coronary plexus was made out in the region of commencement of the bundle. The bundle passed from the posterior part of the base of the auricular septum into the depth of the ventricular septum, where it inclined towards the endocardium on the left side of the septum. Whilst in the ventricular septum the bundle gave off a branch to the muscular valve at the right auriculo-ventricular orifice, this branch the author regards as the homologue of the right limb of the mammalian bundle. Ohmori (15) found the auriculo-ventricular node present in the bird's heart in the lower part of the auricular septum and from it a bundle of specialised muscles passes into the depth of the ventricular septum where it divides into right and left branches which pass to the corresponding sides of the septum. In addition to this main bundle, Ohmori describes "four allied systems" as follows: (*a*) a specialised bundle passing from the A.-V. node to the posterior part of the muscular valve; (*b*) a specialised bundle running from the connective tissue at the root of the aorta through the anterior wall of the right auricle to the free border of the muscular valve where it joins system (*a*), the free border of the valve being regarded as the border line between the right auricle and ventricle, and systems (*a*) and (*b*) forming accessory auriculo-ventricular connections; (*c*) a specialised bundle running from the bifurcation of the main bundle upwards through the ventricular septum to the root of the aorta where it joins system (*b*); (*d*) a peri-arterial collection of Purkinje fibres accompanying the arteries through the ventricular myocardium. Holmes (16) found numerous Purkinje fibres in *both auricles* of many birds, both in the sub-endocardial connective tissue, around arteries in the myocardium and to a slight extent in the epicardium. In the smaller birds' hearts the Purkinje fibres showed only very slight histological differentiation from ordinary cardiac muscle and were recognisable only under high magnification. Holmes is of the opinion that these fibres do not form the path of conduction of the stimulus to contraction in the auricles.

PERSONAL OBSERVATIONS

The results of the present study are based upon the histological investigation of the hearts of the black swan and pigeon in particular. Serial sections (transverse) of these hearts were examined and special blocks from the hearts of the ostrich, stork, black crake and king penguin were also studied. In view of the failure of Mackenzie and Robertson (4) to find a specialised conducting system in the pigeon heart, and bearing in mind the statement of Holmes (16) concerning the slight degree of differentiation of the auricular Purkinje fibres from the myocardium in the hearts of the smaller birds, it was deemed advisable to feed some pigeons well for some time (ten days) prior to removal of the heart in the endeavour to increase the glycogen content of the special conducting system in the hope that this would render the histological difference between the conducting system and the ordinary cardiac muscle more marked. With this preliminary treatment the special conducting system of the pigeon heart was found to be markedly differentiated from the cardiac muscle. The present work is an attempt at a complete study of the topographical disposition of the avian Purkinje system. An endeavour is also made to correlate the peculiar and intricate detail of this system with the functional requirements of the bird's heart. Finally the conducting system of the avian heart thus determined is compared with the present conception of that of the fish and reptile heart on the one hand and with that of the mammalian heart on the other.

DISTRIBUTION OF THE CONDUCTING SYSTEM IN THE BIRD'S HEART

A. *Specialised connections between auricle and ventricle*

The specialised connections between auricle and ventricle are:

1. Auriculo-ventricular node and bundle;
2. Right auriculo-ventricular ring of Purkinje fibres.

1. *The auriculo-ventricular node* (Plate I, fig. 1) is embedded in connective tissue in the lower and posterior part of the auricular septum, a short distance in front and to the left of the opening of the left superior vena cava, a position similar to that occupied by Tawara's node in the mammalian heart. It is ovoid in shape and its lower and anterior part narrows into the commencement of the A.-V. bundle, though it is difficult to demarcate with certainty where node ends and bundle begins owing to similarity of structure. The lower part of the node consists of cells which are larger than the auricular myocardial cells proper, which do not stain so deeply as the myocardium and in which the longitudinal fibrillae are limited to the periphery. The cells are frequently seen to be multinucleated, the nuclei (usually two in number) being rounded

in shape and central in position. The cells in the lower part of the node are more compactly arranged than those in the upper part. The upper part of the node consists of cells, smaller in size, multinucleated, with longitudinal fibrillae only at the periphery, and arranged in strands which are separated from each other by connective tissue. These strands become directly continuous with the ordinary auricular myocardium, but no direct continuity with the Purkinje fibres of the right auricle was observed. The node is surrounded by connective tissue (which is continuous with the auriculo-ventricular fibrous rings and trigonum fibrosum) in which many blood vessels are embedded. Numerous small ganglia and nerve fibres lie in the epicardium immediately superficial to the nodal region. No nerve cells were seen in the node but many nerve fibres penetrate into the perinodal connective tissue. With the stains employed, viz. haematoxylin and eosin, and van Gieson and iron haematoxylin, nerve fibres are not conspicuous in any part of the avian conducting system, though they may be difficult of recognition, especially if non-medullated. This question is being investigated by the use of special stains and will be dealt with in a later communication.

The auriculo-ventricular bundle (Plate I, fig. 2) commences as a narrow rounded bundle continuous with the lower and anterior end of the A.-V. node in the trigonum fibrosum. It soon broadens out and runs forwards and to the left into the depth of the ventricular septum. Thence it passes downwards, forwards and to the left, deeply embedded in the ventricular septum, to a point slightly below and to the right of the anterior septal attachment of the muscular right A.-V. valve. This site is about one-fifth to one-quarter of the distance from the base to the apex of the ventricular septum, and here the bundle, lying midway between the right and left surfaces of the septum, divides into its two limbs, right and left. The bifurcation of the bundle (Plate I, fig. 4) lies deep to (i.e. on the left side of) the main septal division of the right coronary artery, only a thin layer of septal myocardium intervening between the artery and the bifurcation of the bundle, but no communications could be traced between the Purkinje fibres of the bundle and the collection of Purkinje fibres around the septal artery. The main A.-V. bundle consists of large cells, compactly arranged, with longitudinal fibrillae at the periphery and usually two rounded central nuclei. The cells vary in size in various parts of the bundle, tending to be bigger towards the bifurcation and smaller at the constricted commencement of the bundle. The connective tissue about the A.-V. node is continued around the main bundle only to a very slight extent. There is not the same compact sheath (Plate I, fig. 3) around the avian bundle such as is seen in relation to the mammalian bundle (especially in the hearts of Ungulates). In most of the birds' hearts examined there is no connective tissue at all around the bundle, so that its peripheral fibres lie in direct apposition with the septal myocardial fibres and, indeed, may be seen to pass into direct continuity with them. Blood vessels are scanty in the bundle, its vascularity being much less than that of the myocardium. Nerve fibres are not conspicuous with the stains employed.

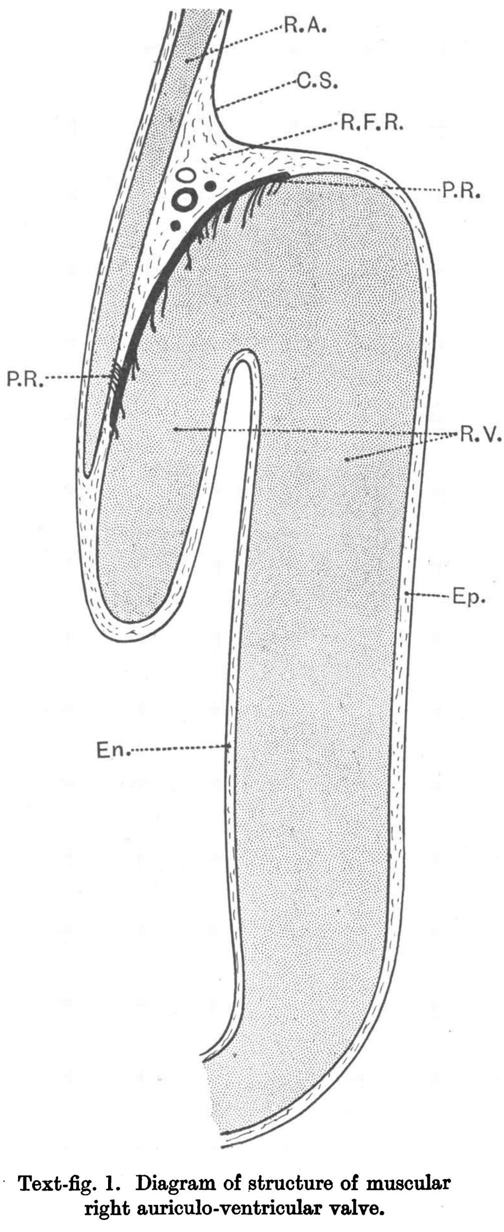
Right limb of the A.-V. bundle (Plate I, fig. 5). From the bifurcation of the main bundle the right limb runs downwards and slightly forwards, at the same time approaching the endocardium on the right side of the septum. It passes in front of and close to the main septal artery, but no fibres appear to pass directly from the right limb to the collection of Purkinje fibres around the artery. At its commencement the right limb is broad, flat and compact, but as it approaches the endocardium it becomes rounded and its component fibres more loosely arranged. After a short course the right limb reaches the sub-endocardial connective tissue on the right side of the septum, where it spreads out (Plate I, fig. 6) and becomes continuous with the sub-endocardial network of Purkinje fibres. The cells of which the right limb consists have the same characters as those of the main bundle, and as in the case of the latter, a connective tissue sheath is absent, the peripheral specialised fibres of the right limb being directly continuous with the neighbouring septal myocardial fibres. Further, as the right limb approaches the endocardium, strands of ordinary myocardial fibres actually pass transversely through the limb between the specialised fibres (Plate II, fig. 7). As it nears the endocardium, the right limb gives off a small rounded branch (Plate II, fig. 8) composed of loosely arranged Purkinje fibres, which runs upwards and to the left immediately beneath the endocardium, to enter the muscular valve at its anterior septal attachment. This is the first branch given off from the right limb and its distribution to the muscular right auriculo-ventricular valve suggests that this valve *actively* contracts *early* in ventricular systole, so allowing exit for the blood from the right ventricle through the pulmonary artery alone during the greater part of systole of the ventricle. As far as the present writer is aware, it is unknown at what exact period of the cardiac cycle this muscular valve comes into operation and it is proposed to investigate this question experimentally. In the exceedingly rapid hearts of small birds it is evident that ventricular systole is of very short duration, and that for transmission of the greater part of the ventricular blood through the pulmonary artery during systole the auriculo-ventricular orifice must be closed almost at the outset of systole. If the above suggestion is correct it represents an interesting example of adaptation of structure to function in the rapidly beating bird's heart. This branch to the muscular valve was described by Drennan (14) in the ostrich, and he regarded it as the homologue of the right limb of the mammalian bundle, but it is clear that it is only a branch of the right limb of the avian bundle, the latter itself being the true homologue of the right limb of the mammalian bundle.

Left limb of the A.-V. bundle (Plate I, fig. 5). From the bifurcation of the main bundle the left limb runs downwards and, after a short course, reaches the sub-endocardial connective tissue on the left side of the ventricular septum (Plate II, fig. 9), where it spreads out to become continuous with the network of Purkinje fibres beneath the endocardium. From its commencement the left limb assumes the form of a broad flattened band of compactly arranged fibres, but as it approaches the endocardium the fibres become more loosely arranged as they diverge to become continuous with the sub-endocardial Purkinje network. There is no connective tissue sheath around the left limb, the peripheral specialised fibres establishing continuity with the neighbouring myocardium. The cells of which the left limb consists have the same histological characters as those of the main bundle; they tend to get larger as the endocardium is approached. In both right and left limbs, as in the case of the main bundle, blood vessels and (with the stains used) nerve fibres are conspicuous by their absence.

Special recurrent branch of the A.-V. bundle. From the point of its bifurcation the main A.-V. bundle gives off a branch which runs upwards, forwards and to the left in the depth of the ventricular septum (Plate II, fig. 10). It takes the form of a rounded bundle in which the Purkinje fibres are compactly arranged, and about which there is no connective tissue sheath, the peripheral specialised fibres establishing continuity with the neighbouring septal myocardium. The branch rapidly diminishes in size as it approaches the base of the ventricular septum, where it lies in the septal myocardium in front of the mitral orifice. Thence it passes upwards, as a very small bundle, in the myocardium on the anterior and left aspect of the root of the aorta, where it receives communications from the peri-arterial collections of Purkinje fibres about the neighbouring branches of the left coronary artery. Finally it passes backwards (Plate II, fig. 11) in the connective tissue on the left side of the root of the aorta and ends by joining the aortic end of the bundle of Purkinje fibres, which passes from the auriculo-ventricular node around the right auriculo-ventricular orifice, behind the root of the aorta.

2. *Right auriculo-ventricular ring of Purkinje fibres.* A study of the structure of the muscular right auriculo-ventricular valve reveals that it consists chiefly of an inflection of the ventricular myocardium, with a much smaller inner layer of auricular muscle (text-figure 1). The auricular myocardial component of the valve does not reach down as far as the lower free border of the valve in any part of its circumference, but extends downwards on the inner aspect of the ventricular myocardial component for varying distances in different parts of the valve. Between these two myocardial components of the valve there is a collection of fibrous tissue which is really part of the right auriculo-ventricular fibrous ring, the invaginated condition of the muscular and fibrous constituents of the valve having been produced by the upward expansion of the ventricle. From the lower and posterior part of the auriculo-ventricular node (Plate II, fig. 12) a small bundle of Purkinje fibres is given off, which passes at first backwards and to the right, in the right auriculo-ventricular fibrous ring, into the fibrous tissue between the auricular and ventricular components of the muscular valve. In this connective tissue it expands into the form of a sheet of Purkinje fibres (Plate III, fig. 13) which

passes forwards and subsequently to the left, finally leaving the valve by passing into the connective tissue on the right side of the root of the aorta (Plate III, fig. 14). Here it again assumes the form of a small rounded bundle, and inclines backwards to join the aortic end of the recurrent branch of the main auriculo-ventricular bundle in the connective tissue on the back of the root of the aorta. On its way round the right auriculo-ventricular orifice, in the fibrous tissue between the auricular and ventricular myocardial components of the valve (Plate III, fig. 15), this sheet of Purkinje fibres establishes continuity with both auricular and ventricular myocardial parts of the valve, thus constituting accessory auriculo-ventricular connections. This special auriculo-ventricular ring of Purkinje fibres comes into intimate association with the numerous small ganglia and nerve fibres in the connective tissue at the base of the valve. Likewise in the connective tissue at the base of the aorta, the terminal parts of the recurrent branch of the main A.-V. bundle and of the special ring of Purkinje fibres are very intimately related to the ganglia and nerve fibres in this situation.



Text-fig. 1. Diagram of structure of muscular right auriculo-ventricular valve.

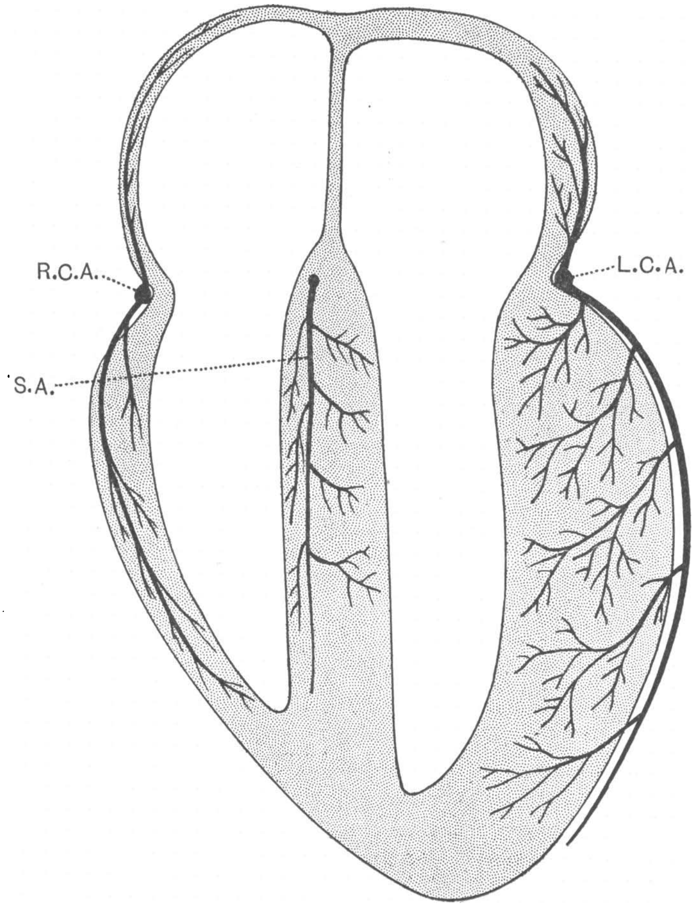
B. *Distribution of the Purkinje fibres in the ventricles*

The Purkinje fibres have a very extensive and intricate disposition in the ventricular walls, being found beneath the endocardium, around arteries in the myocardium, and to a lesser extent in the epicardium. The detailed architecture of this Purkinje system has up to the present remained untraced.

1. *Ventricular sub-endocardial Purkinje fibres.* The right and left limbs of the main A.-V. bundle have been shown above to pass to the sub-endocardial connective tissue on the right and left sides respectively of the ventricular septum, where they spread out and are continued into the sub-endocardial Purkinje network. The fibres of this latter network run downwards towards the apex of the heart, and also radiate to right and left on each side of the septum to reach the sub-endocardial network on the free walls of the ventricles at the region of septal attachment, this arrangement being similar to that which occurs in the case of the *left* limb only of the mammalian bundle. No sub-endocardial Purkinje fibres are found on either side of the ventricular septum above the level at which the right and left limbs of the A.-V. bundle reach the sub-endocardial connective tissue, except at the junction of the septum and free wall of each ventricle, where some of the radiating Purkinje fibres may curve upwards to reach slightly higher than the level of commencement of the network on the septum. On the free wall of the right ventricle the sub-endocardial Purkinje fibres pass up to the attachment of the muscular valve, and also extend for a short distance on to its ventricular surface. They do not form auriculo-ventricular connections over the free border of the valve with the sub-endocardial Purkinje fibres of the right auricle. Only a few sub-endocardial Purkinje fibres are found in the lower part of the conus arteriosus and none at all in its major portion. The sub-endocardial Purkinje fibres on the free wall of the left ventricle run up as far as the attachment of the mitral valve, but stop short some distance from the aortic valve. They are entirely independent of the sub-endocardial Purkinje fibres of the left auricle and form no connections with them. It is to be noted that in most places the sub-endocardial Purkinje fibres lie in contact with the subjacent myocardial fibres proper, the main thickness of the sub-endocardial connective tissue lying between them and the endocardial lining of the ventricles. In many places, however, they are embedded in the sub-endocardial connective tissue. The sub-endocardial Purkinje fibres are most numerous on the free wall of the left ventricle, where in many places they form practically a continuous layer (as seen in transverse sections of the heart) (Plate III, fig. 16). The cells are very much larger than the myocardial cells, and frequently show two nuclei which are rounded in shape and central in position. Longitudinal fibrillae are few in number and are limited to the periphery of the cell. The size and structure of these Purkinje cells markedly differentiate them from the adjacent myocardium. From the sub-endocardial Purkinje network, both on the septum and on the free walls of both ventricles, Purkinje fibres penetrate into the adjacent myocardium and become continuous with either the ordinary myocardial fibres directly or with the peri-arterial collections of Purkinje fibres about the myocardial branches of the coronary arteries. These penetrating strands of Purkinje fibres are especially marked in the free wall of the left ventricle, and arise from the sub-endocardial network chiefly in the sulci between the trabeculae carneae.

2. *Peri-arterial Purkinje fibres in the ventricular walls.* As above described, strands of Purkinje fibres penetrate from the sub-endocardial network into the adjacent myocardium. Most of these penetrating strands become continuous with the collections of Purkinje fibres around the myocardial branches of the coronary arteries (Plate III, fig. 17), and are conducted along these arteries throughout the thickness of the myocardium towards the epicardial surface (Plate III, fig. 18), the fibres on their way establishing continuity with the myocardial fibres at various depths from the surface. All the peri-arterial collections of Purkinje fibres appear to be derived from the sub-endocardial networks in the various regions of the heart wall, and, conducted along the myocardial branches of the coronary arteries, they form an intricate intramyocardial system of conducting fibres, establishing continuity with the ordinary cardiac muscle at numerous sites along their course. In some places the fibres follow the arteries right through the thickness of the myocardium into the epicardial connective tissue, this being especially the case in the free wall of the left ventricle, where peri-arterial Purkinje fibres are found about the main branches of the left coronary artery as they lie in the epicardium in the region of the anterior interventricular sulcus. A clue to the detailed architecture of this intricate peri-arterial Purkinje system is obtained by a study of the "pattern" of the myocardial branches of the coronary arteries in the walls of the various chambers of the heart (text-figure 2). The type of pattern is found to vary with the varying thickness of the cardiac wall. In the case of the very thick free wall of the left ventricle, the descending branches of the left coronary artery, which lie in the epicardium, give off twigs which enter the myocardium at a wide angle and arborise throughout the thickness of the wall in a tree-like manner. In the thinner free wall of the right ventricle, twigs from branches of the right coronary artery enter the myocardium at an acute angle and only gradually sink into the depth of the wall. In the thin walls of the auricles (especially the right) the arteries only very gradually sink into the depth of the myocardium, the smaller twigs running more or less parallel with the surface. In a similar manner the main arteries descending in the ventricular septum lie between a thin right and a thick left layer of the septal musculature, and the branches passing towards the endocardium on the left side of the septum have thus a "tree-pattern" of distribution like those in the thick free wall of the left ventricle, whilst those passing towards the right side of the septum follow a "parallel-pattern" and only gradually pass through the thin right layer of the septum. It is thus evident that in the case of the thick free wall of the left ventricle and of the thick left layer of the ventricular septum the branches of the coronary arteries take a comparatively *short course* through the thick muscular layer. The peri-arterial Purkinje fibres in the ventricular walls are independent of those in the auricular walls and do not afford a means of specialised connections between auricles and ventricles. In the ventricular septum, below the level of the commencement of the sub-endocardial Purkinje networks on either side,

the branches of the septal arteries passing towards the right and left surfaces of the septum are surrounded by Purkinje fibres derived from the right and left sub-endocardial networks respectively. The peri-arterial Purkinje fibres about the main septal artery as it lies in the septum above the level of the bifurcation of the main A.-V. bundle are derived from the sub-endocardial



Text-fig. 2. Diagram of pattern of coronary arteries of bird's heart. (For explanation see text.)

network on the right side of the septum lower down and are passing upwards to become continuous with the myocardium of the upper and right part of the septum. This recurrent arrangement of these peri-arterial Purkinje fibres is comparable to that of the recurrent branch given off from the A.-V. bundle at its bifurcation, many of whose fibres become continuous with the myocardium of the upper and left part of the ventricular septum. As the main septal artery (i.e. the main branch of the right coronary artery) is passing downwards and backwards in the upper part of the ventricular septum, at the sites where it lies subjacent to the anterior and posterior septal attachments of the muscular valve, it gives off branches, surrounded by Purkinje fibres, to this valve. In the conus arteriosus the peri-arterial Purkinje fibres are derived from the sub-endocardial Purkinje fibres of the adjacent part of the right ventricle, and they are arranged about branches of the third coronary artery. This is the last coronary artery given off from the aorta and it is entirely expended upon supplying the part of the right ventricle that has been shown by Lewis to contract last, viz. the conus.

C. *Distribution of Purkinje fibres in the auricles*

As in the walls of the ventricles, Purkinje fibres have an extensive and complicated arrangement in the auricular walls, and are found beneath the endocardium, around arteries in the myocardium and in some places in the epicardium. Sub-endocardial Purkinje fibres (Plate IV, fig. 19) are found throughout both auricles, but are relatively scarce on the auricular septum. They become less numerous in the lower parts of the auricular walls and stop short some distance above the auriculo-ventricular valves. They do not constitute special auriculo-ventricular connections, but are independent of those in the ventricular walls. As in the case of the ventricular system, branches from the sub-endocardial Purkinje fibres penetrate into the auricular myocardium around the auricular branches of the coronary arteries, and in some places the peri-arterial Purkinje fibres pass through the entire thickness of the auricular wall into the sub-epicardial connective tissue. This auricular peri-arterial system of Purkinje fibres is independent of the ventricular peri-arterial system, and no connections could be traced between them.

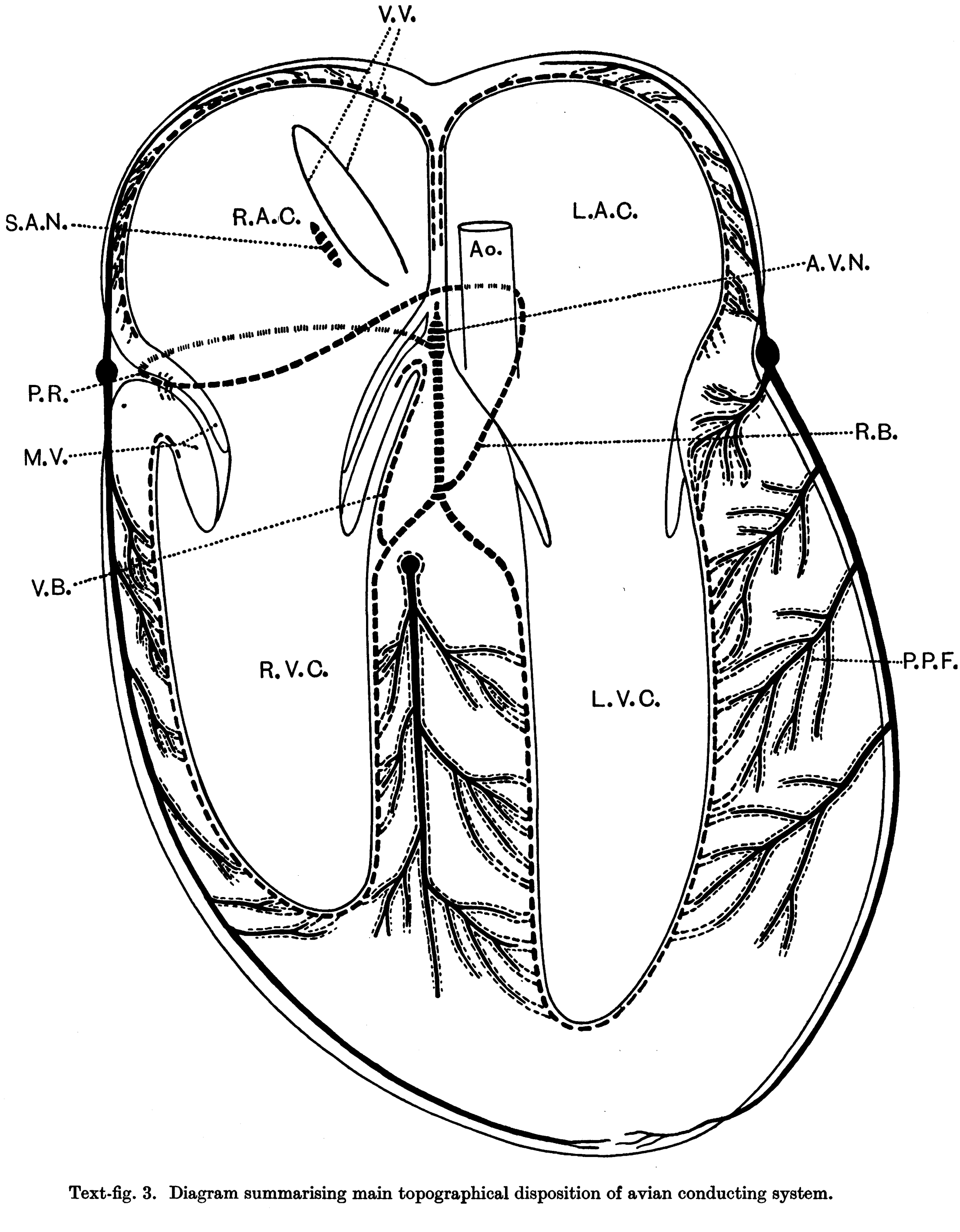
Sinu-auricular node (Plate IV, fig. 20). Beneath the epicardium at the base of the right venous valve there is a mass of fibres which does not stain so deeply as the adjacent myocardium. This mass is widest in its middle and tapers off above and below. It extends upwards from just above the orifice of the inferior vena cava to a point some distance below the opening of the right superior vena cava. It is composed of fibres (Plate IV, fig. 21) in which the longitudinal fibrillae are limited to the periphery, the central parts of the fibres being very clear and staining very pale. In many of the cells of which the fibres consist, two nuclei, centrally situated and round in shape, can be seen. The fibres form intricate inter-crossings and interspersed between them there is a fair amount of connective tissue. For the most part the fibres are larger than the ordinary auricular myocardial fibres; smaller fibres are in a minority. The fibres are continuous with the adjacent ordinary cardiac muscle of the right auricle. They appear also to establish continuity with the sub-endocardial Purkinje fibres in the neighbourhood. No nerve cells are present in the mass itself, but small ganglia and nerve fibres are plentiful in the epicardial connective tissue in this region, and nerve fibres can be traced towards the mass but are not conspicuous in the mass itself. Two branches of the right coronary artery run longitudinally, one in front of and one behind the mass, and an anastomosing vessel connecting these two arteries passes through the mass, an arterial arrangement very similar to that which occurs in the region of the sinu-auricular node in the mammalian heart. The above morphological data are evidence that the lightly staining ovoid mass in the base of the right venous valve is the avian sinu-auricular node. Confirmation will be sought by future experimental work.

DISCUSSION

The conducting system of the avian heart (text-figure 3) is seen from the present investigation to consist mainly of:

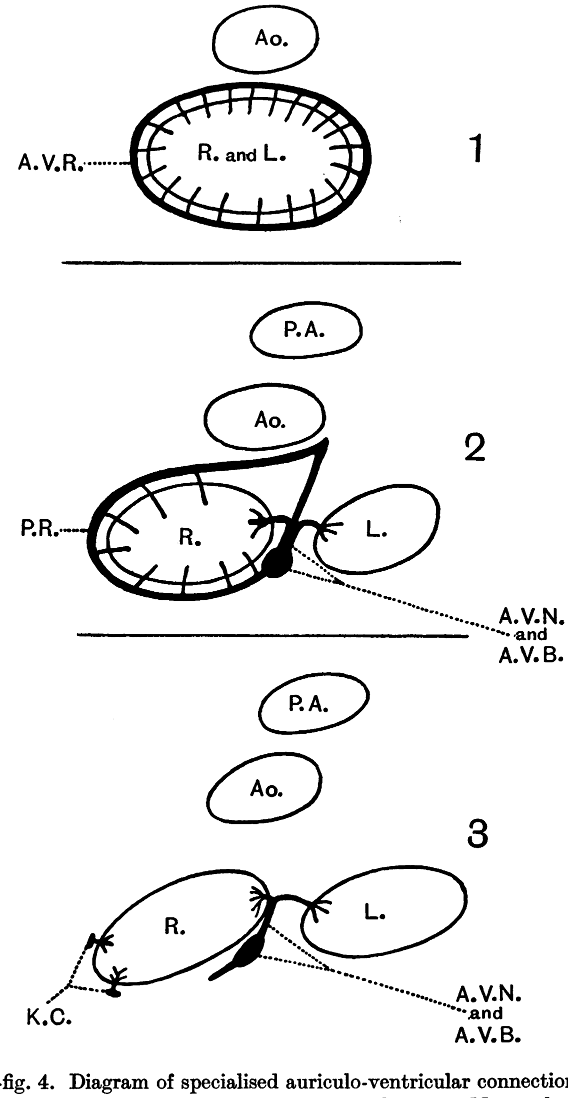
(*a*) sinu-auricular node, and auricular sub-endocardial and peri-arterial Purkinje ramifications; and

(*b*) auriculo-ventricular node, and right auriculo-ventricular ring of Purkinje fibres, both establishing connections between auricle and ventricle, the A.-V. node by means of the auriculo-ventricular bundle and its two limbs ending in the ventricular sub-endocardial and peri-arterial Purkinje ramifications, and the right auriculo-ventricular ring of Purkinje fibres by means of its connections with the auricular and ventricular myocardial components of the muscular valve. It is interesting and instructive to compare the special auriculo-ventricular connections of the bird's heart thus determined, with those of the mammalian heart on the one hand and with those of the fish and reptilian heart on the other (text-figure 4). In the fish and lower reptile heart a ring of specialised fibres (auriculo-ventricular ring), at the junction of auricle and ventricle, establishes continuity between these chambers of the heart in its entire circumference. In the mammalian heart, with the development of *membranous* auriculo-ventricular valves and auriculo-ventricular fibrous rings, the auriculo-ventricular ring of special tissue becomes reduced or narrowed, and the remaining connection between auricle and ventricle is represented by the auriculo-ventricular node, the auriculo-ventricular bundle and its two limbs being developed in association with the separation of the ventricles by a septum. (There is some evidence, however, that the A.-V. node is a derivative of the sinu-auricular, and not of the auriculo-ventricular ring, namely, that the right vagus and the right sympathetic are associated experimentally with the sinu-auricular node, and the left vagus and left sympathetic with the auriculo-ventricular node, both nodes being considered thus to be derivatives of the sinu-auricular ring.) It is possible that the accessory auriculo-ventricular connections described by Stanley Kent (17), and confirmed by Todd and van der Stricht (18 and 19), are persistent derivatives of the auriculo-ventricular ring. In the avian heart, the auriculo-ventricular node and the auriculo-ventricular bundle with its two limbs have been developed, and in addition the auriculo-ventricular ring to some extent retained. The avian auriculo-ventricular connections thus present an arrangement intermediate between those of the fish and reptile and those of the mammal. The



Text-fig. 3. Diagram summarising main topographical disposition of avian conducting system.

persistence of the special auriculo-ventricular ring is to be correlated with the muscular structure of the right auriculo-ventricular valve, and the auriculo-ventricular bundle and its divisions with the complete separation of the ventricles by a septum; the distribution of one limb to each ventricle is



Text-fig. 4. Diagram of specialised auriculo-ventricular connections in:
1. Fish and lower reptile; 2. Bird; 3. Mammal.

correlated with the simultaneous contraction of the two ventricles. The arrangement of the special tissue at the sinu-auricular junction also differs in the above species. In the fish heart there is a ring of special tissue (sinu-auricular ring) at the bases of the venous valves. In the reptilian (lizard) heart specialised muscle at the sinu-auricular junction is limited to the base of the *left* venous valve, whereas in the mammalian heart it is limited to the upper part of the base of the right venous valve (upper part of sulcus terminalis). In the avian heart specialised muscle at the sinu-auricular junction is found in the base of the right venous valve, but relatively nearer the orifice of the inferior vena cava than in the mammalian heart. In addition to the above morphological variations in the conducting system of different species of animals, another factor controls the amount and extent of distribution of the Purkinje system, namely, the *rate of the heart beat.* The extensive distribution of the avian Purkinje system, both auricular and ventricular, sub-endocardial and peri-arterial, is correlated with the rapid heart rate in the bird. The patterns of the myocardial branches of the coronary arteries have been shown above to vary with the thickness of the cardiac wall, and in the case of the very thick free wall of the left ventricle, for instance, it is evident that the "tree-pattern" of distribution of the coronary arteries enables the peri-arterial Purkinje fibres to take a relatively short course through the thick myocardium. This accounts for the rapidity of arrival of the wave of excitation at a given point on the surface of the left ventricle wall in the bird's heart, as observed by Lewis (10).

The absence of a fibrous sheath about the avian auriculo-ventricular bundle and its divisions is similarly to be correlated with the rapidity of the heart rate, the necessity arising for early and widespread diffusion of the impulse from the auricle along the bundle to all parts of the ventricles, with consequent early and widespread continuity of the bundle and its divisions with the myocardium. The absence of a fibrous sheath about the bundle in the rapidly contracting avian heart also suggests the part played by the fibrous sheath about the mammalian A.-V. bundle. Lhamon (20) confirms the description of Tawara, who demonstrated that the fibrous sheath around the mammalian A.-V. bundle can be traced along the divisions of the bundle and the terminal Purkinje fasciculi to blend with the perimysium of the cardiac muscle where the Purkinje fibres blend with the myocardial fibres, thus isolating completely the conducting system from the neighbouring myocardium. This fibrous sheath can be injected with fluids like indian ink or prussian blue, and these injections demonstrate that the potential space between the sheath and the bundle is not continuous with the lymphatic system of the heart. Curran (21) described a "constant mucous bursa" about the mammalian A.-V. bundle, containing a fluid somewhat more viscid than lymph, and he attributed to the fibrous sheath a mechanical protective action in that it would diminish friction between the vigorously contracting myocardium and the *relatively* stationary bundle. If this were the function of the fibrous sheath, then, in the rapidly and vigorously contracting avian heart, where the A.-V. bundle is deeply embedded in the thick ventricular septum, a well-developed protective fibrous sheath would be expected to be present. The absence of an avian sheath, correlated as above stated with the rapidity of the heart rate in the bird, suggests that the mammalian sheath, in the slower heart, is concerned with insulation of the bundle and its branches from the neighbouring myocardium. An analogy can be drawn between this action of the mammalian sheath and the insulating action of the neurilemma (Trotter (22)), which, for example, in the case of the motor nerve, insulates the axis cylinder right up to the region of continuity of conducting and contractile tissue.

The intimate relation between the aortic ends of the right auriculo-ventricular Purkinje ring and of the recurrent branch given off from the bifurcation of the main A.-V. bundle and the numerous small ganglia and nerve fibres at the base of the aorta, raises the question as to whether the Purkinje system plays any part at all on the *afferent* side of cardiac control. The recurrent branch of the main A.-V. bundle, given off at its bifurcation, and passing up through the ventricular septum just in front of the mitral valve, recalls the original description by His (23) of the left limb of the mammalian A.-V. bundle terminating in the base of the aortic (anterior) cusp of the mitral valve. Such an aberrant left branch has been described in abnormal human hearts (Morison (24)), and frequently in normal human hearts an abruptly ending process can be traced in this direction (Walmsley (25)).

SUMMARY AND CONCLUSIONS

1. The conducting system, of specialised structure, of the avian heart is described.
2. The special auriculo-ventricular and sinu-auricular connections in the bird's heart are compared with our present conception of those in the fish, reptilian and mammalian heart.
3. The extensive distribution of the avian Purkinje system is correlated with the rapidity of the heart rate.
4. The structure of the muscular right auriculo-ventricular valve is described, together with its influence upon the configuration of the conducting system.
5. The absence of a well-defined fibrous sheath about the avian bundle is noted, and its bearing upon the probable insulating action of the mammalian sheath is discussed. The absence of a sheath is also correlated with the rapidity of heart rate.

The above work was carried out in the Anatomical Department, University College, London. My thanks are due to my chiefs, Prof. G. Elliot Smith and Prof. J. P. Hill, for advice throughout the course of the work, also to Mr E. O. Lloyd, technical assistant, who prepared the microscopic sections, and to Mr F. Pittock, who prepared the microphotographs and lantern slides. The birds' hearts were kindly given me by Mr S. Zuckerman, Anatomist at the Gardens of the Zoological Society, London.

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DESCRIPTION OF PLATES I–IV

PLATE I

Fig. 1. Oblique section through posterior part of junction of auricular and ventricular septum. Low power. Pigeon.

Fig. 2. Oblique section through upper part of ventricular septum. Low power. Black swan.

Fig. 3. Transverse section through upper quarter of ventricular septum. Low power. Black crake.

Fig. 4. Transverse section ventricular septum at level of bifurcation of A.-V. bundle. Low power. Black swan.

Fig. 5. Transverse section ventricular septum just below bifurcation of A.-V. bundle. Low power. Black swan.

Fig. 6. Transverse section ventricular septum below bifurcation of A.-V. bundle, at level where right limb of bundle approaches endocardium. Low power. Black swan.

PLATE II

Fig. 7. Transverse section ventricular septum slightly above level of fig. 6. Low power. Black swan.

Fig. 8. Transverse section ventricular septum a little above level of fig. 7. Low power. Black swan.

Fig. 9. Transverse section ventricular septum at level where left limb of bundle approaches endocardium. Low power. Black swan.

Fig. 10. Transverse section ventricular septum above level of bifurcation of bundle. Low power. Black swan.

Fig. 11. Transverse section of aorta. Low power. Pigeon.

Fig. 12. Transverse section at junction of right auricle and ventricle. Low power. Pigeon.

PLATE III

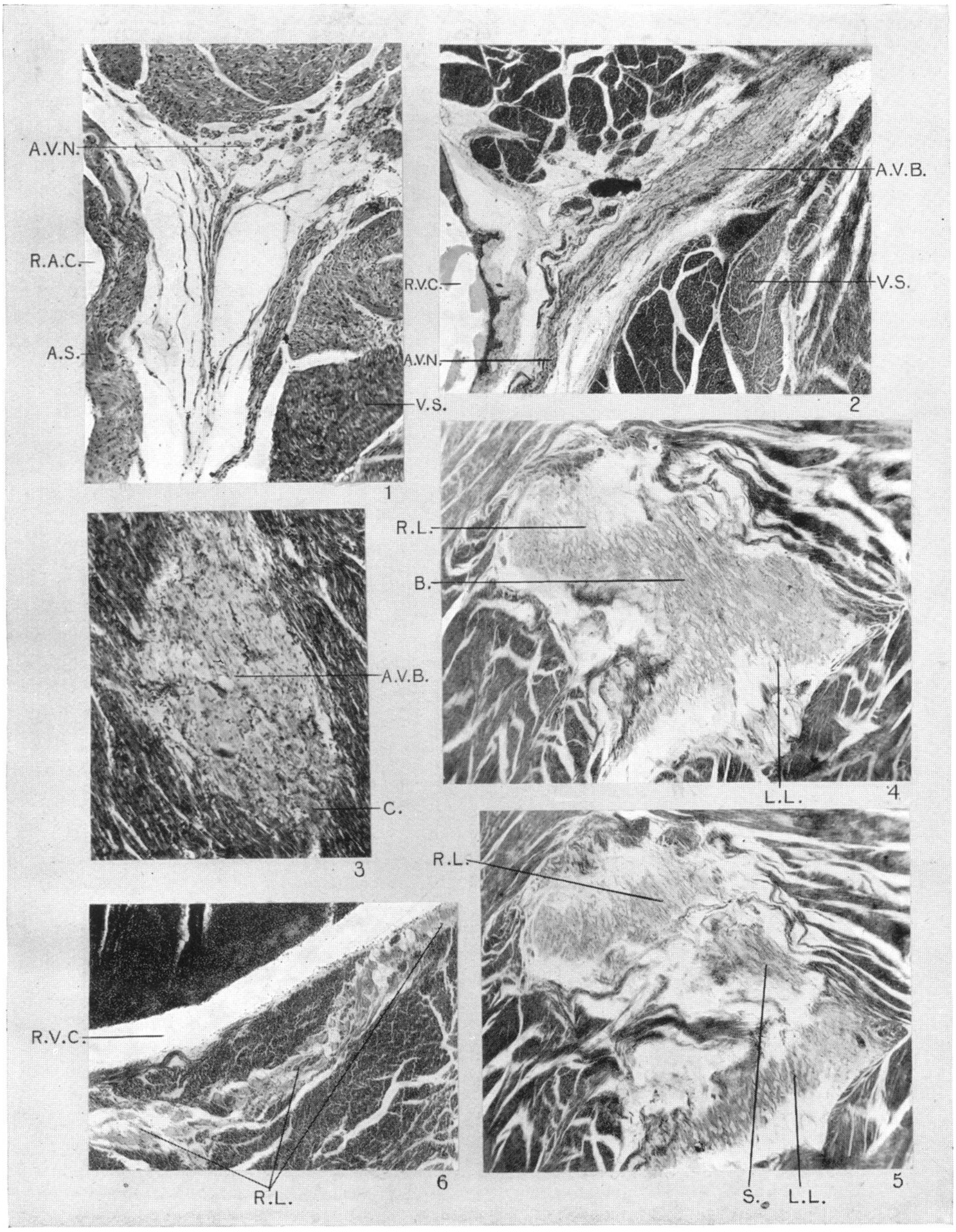
Fig. 13. Longitudinal section muscular valve. Low power. King penguin.
Fig. 14. Transverse section base of aorta. Low power. Pigeon.
Fig. 15. Transverse section muscular valve. Low power. Pigeon.
Fig. 16. Transverse section lower part left ventricle. Low power. Black swan.
Fig. 17. Transverse section lower part left ventricle. Low power. Black swan.
Fig. 18. Transverse section lower part left ventricle. Low power. Black swan.

PLATE IV

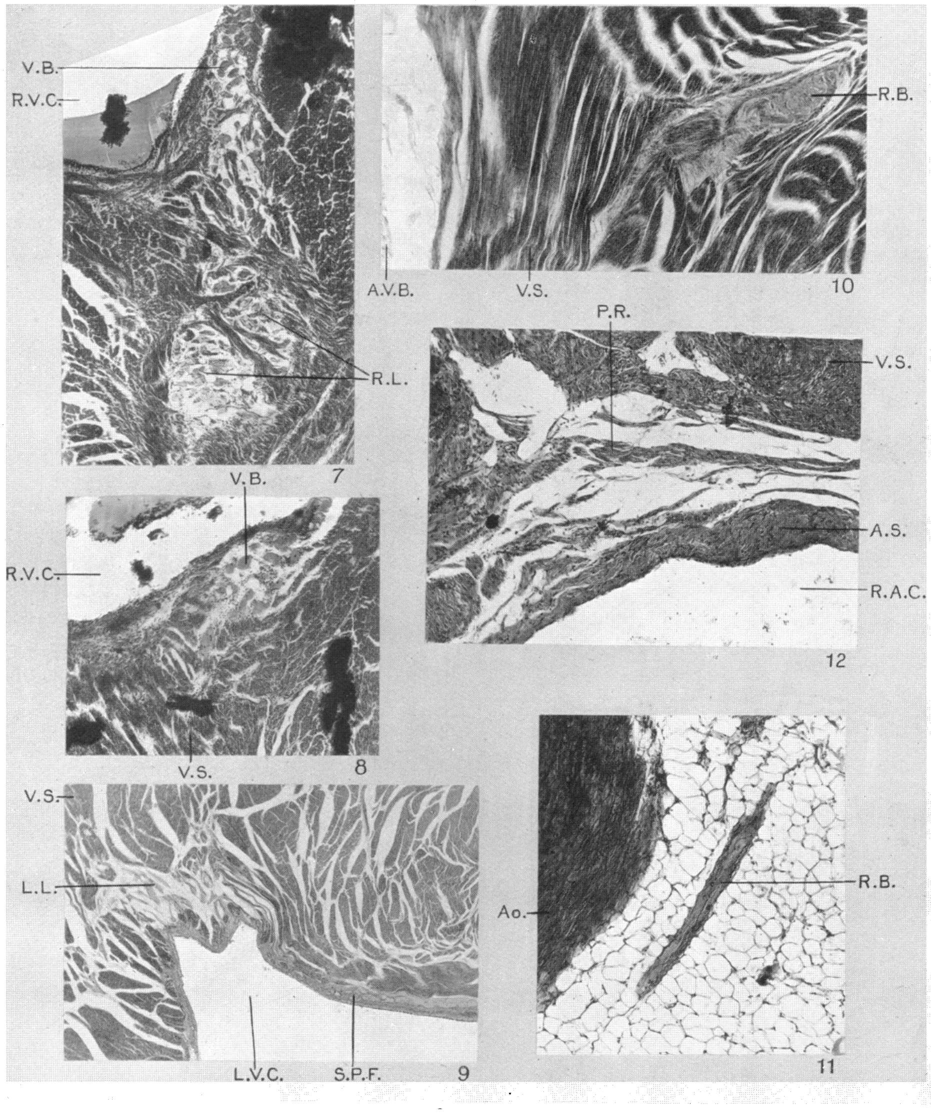
Fig. 19. Transverse section upper part left auricle. Low power. Black swan.
Fig. 20. Transverse section right auricle. Low power. Stork.
Fig. 21. High power view of lighter area in fig. 20. Stork.

ABBREVIATIONS USED IN PLATES AND TEXT-FIGURES

Ao.	Aorta.
A.S.	Auricular septum.
A.V.B.	Auriculo-ventricular bundle.
A.V.N.	Auriculo-ventricular node.
A.V.R.	Auriculo-ventricular ring of specialised muscle.
B.	Bifurcation of A.-V. bundle.
C.	Continuity of Purkinje and myocardial fibres.
C.S.	Coronary (auriculo-ventricular) sulcus.
En.	Endocardium.
Ep.	Epicardium.
K.C.	Accessory auriculo-ventricular connections of Stanley Kent.
L.	Left auriculo-ventricular orifice.
L.A.	Left auricle wall.
L.A.C.	Left auricle cavity.
L.C.A.	Left coronary artery.
L.L.	Left limb of A.-V. bundle.
L.V.	Left ventricle wall.
L.V.C.	Left ventricle cavity.
M.V.	Muscular right auriculo-ventricular valve.
P.A.	Pulmonary artery.
P.F.L.	Purkinje fibre cut longitudinally.
P.F.T.	Purkinje fibre cut transversely.
P.P.F.	Peri-arterial Purkinje fibres.
P.R.	Ring of Purkinje fibres about right auriculo-ventricular orifice.
R.	Right auriculo-ventricular orifice.
R.A.	Right auricle wall.
R.B.	Recurrent branch of A.-V. bundle.
R.A.C.	Right auricle cavity.
R.C.A.	Right coronary artery.
R.F.R.	Right auriculo-ventricular fibrous ring.
R. & L.	Common ventricular orifice.
R.L.	Right limb of A.-V. bundle.
R.V.	Right ventricle wall.
R.V.C.	Right ventricle cavity.
R.V.V.	Right venous valve.
S.	Spur of septal myocardium between right and left limbs of A.-V. bundle.
S.A.	Septal artery.
S.A.N.	Sinu-auricular node.
S.P.F.	Sub-endocardial Purkinje fibres.
V.B.	Branch of right limb of A.-V. bundle to muscular valve.
V.S.	Ventricular septum.
V.V.	Venous valves (right and left).



DAVIES—THE CONDUCTING SYSTEM OF THE BIRD'S HEART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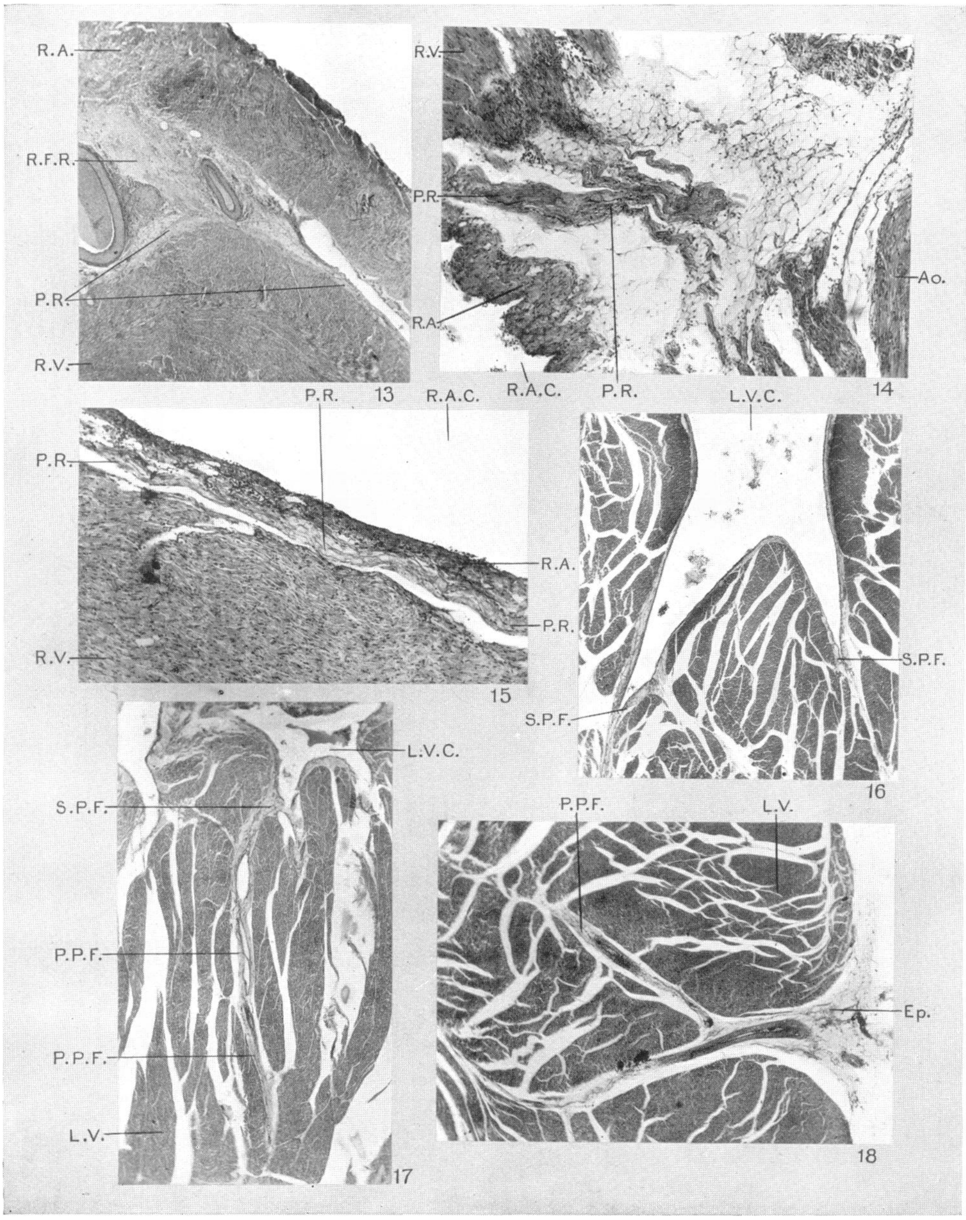
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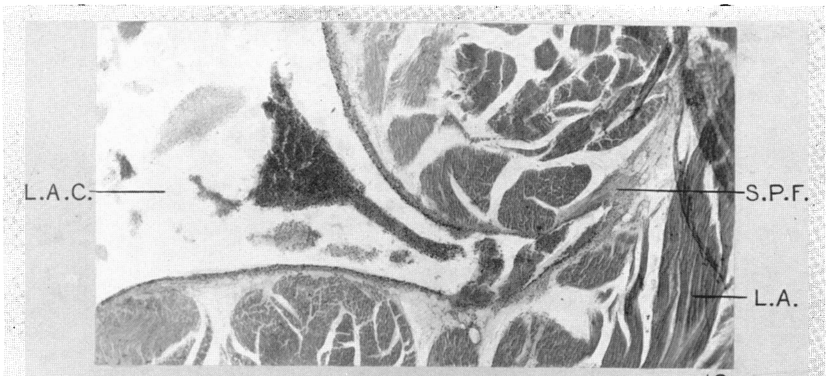

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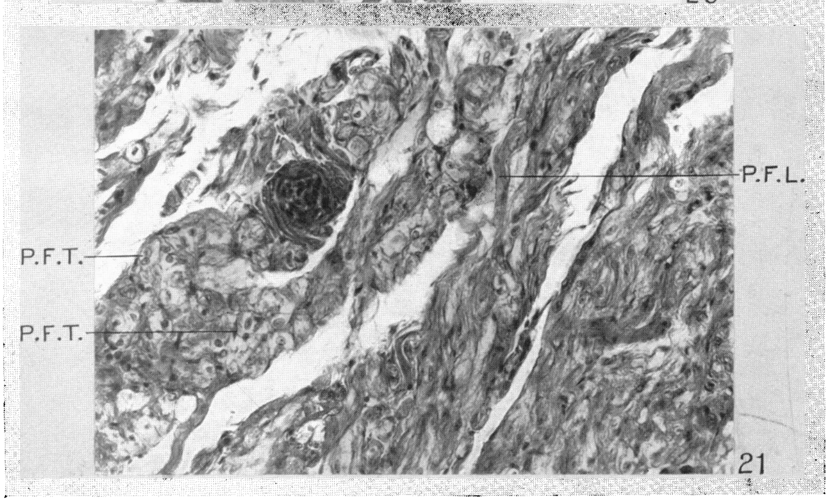

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